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THE MORPHOLGY OF PHYLLAPLYSIA ZOSTERICOLA, NEW SPECIES

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In 1900 Wm. H. Dall of the United States National Museum described *Phyllaplysia taylori* from some specimens sent to him by Rev. Dr. George W. Taylor of Wellington, British Columbia, which Taylor had collected from some floating sea-grass near Nanaimo, B. C. The description was quite brief and there were no illustrations. Dall did not mention a shell and stated that the animal was ". . . translucent, of a uniform pale lemon-yellow color, . . ." Shortly thereafter, Dall sent one specimen to Dr. Rudolph Bergh who redescribed the form in somewhat greater detail in 1902. Bergh included ten figures in his paper, described a shell, and generally agreed with Dall about the color and lack of markings on the animal. Bergh discussed the radula in some detail.

On the west coast of the United States biologists came to know the green, striped tectibranch that is common on the eelgrass of the bays as *Phyllaplysia taylori*, and the species became well known to many of the marine biologists. It is not known who first misidentified the form, but the misidentifica-

tion has been nurtured in the laboratories of the west. The species described by Dall and redescribed by Bergh had a shell and was subsequently removed from the genus *Phyllaplysia* and transferred to *Petalifera* (= *Aplysiella*) by Engel and Hummelinek (1936). Dr. Ernesto Marcus (personal communication) tells me that this is now known correctly at Petalifera petalifera taylori (Dall, 1900). The green, striped form that is well known on the Pacific Coast is without a shell and properly belongs in the genus *Phyllaply*sia. There are a number of other differences between the species described by Dall and the green, striped form. The color of Dall's species was said to be lemon-yellow when preserved in alcohol and to be without markings. The green, striped form is also yellow in alcohol, but the black lines are still visible in some specimens which I have had in alcohol for more than ten years. According to Bergh, Dall's species has a radula with 33 rows of toothplates of 32–34 lateral toothplates on each side of a median toothplate, whereas in the green, striped form the radula consists of 41 rows of toothplates of 50 lateral toothplates on either side of the median toothplate. Furthermore, the median toothplate of Dall's species has two lateral teeth on each side of a pointed median tooth, and the median toothplate of the green, striped species has only one small lateral tooth on either side of the median, lesspointed tooth.

The green, striped form has been misidentified and become well known by the wrong name; as a matter of fact, this relatively common form is to this time unnamed and undescribed. I here propose the name *Phyllaplysia zosteri*cola for its habit of living upon the blades of the broad-leafed celgrass, *Zostera marina*.

Specimens used for this description were collected in Mitchell Bay, San Juan County, Washington. Live specimens were maintained in the laboratory at room temperature, under aeration. The sea water was changed every two or three weeks and the eelgrass likewise changed. I was able to maintain the animals for more than three months in this manner.

Most of the morphology was worked out from dissections under the stereoscopic microscope. Details of the anatomy were worked out with serial sections stained with alum-haematoxylin and triosin. Serial sections of the adult were used for the details of the reproductive system but serial sections of a juvenile proved more satisfactory for most of the other details because of better fixation and better size. Whole mounts of small juveniles were stained with paracarmine and eleared.

Phyllaplysia zostericola McCauley, new species.

SYNONYMS. P. taylori Dall, 1900 of MacGinitie, 1939.

P. taylori Dall, 1900 of Ricketts and Calvin, 1948.

P. taylori Dall, 1900 of MaeGinitie and MacGinitie, 1949.

P. taylori Dall, 1900 of Smith et al., 1954.

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TYPE. The type was collected from the blades of *Zostera marina* at Mitchell Bay, San Juan Island, Washington, in July, 1948. It has been deposited in the collection of the California Academy of Sciences and has been designated as Type No. 8342, Department of Geology, C.A.S.

DIAGNOSIS. Size of the living specimen 50 mm. long by 10 mm. wide, subjeet to great variation. Elliptical, of a pale green color with dorsal longitudinal white stripes edged with black stippling. Stripe next to edge of foot lacks stippled margin. Foot of uniform green color. Anterior end continues into two leaflike tentacles with lateral slits. Pair of rhinophores posteromedially to two small eyes. Foot broad, continuous with body and separated from head by "gutter." No anterior notch in foot. Penis cavity anterior to base of right rhinophore, penis unarmed. Right parapodium folds over left to cover branchial cavity. Opening of genital pore anterior to incurrent opening of branchial cavity on dorsal body surface. Seminal groove from genital pore to penis cavity. Shell absent. Ctenidium single. Radula of 40–41 rows of teeth with 42–52 lateral teeth on either side of rachidial tooth. Rachidial tooth with one small lateral cusp on each side of a slightly larger median cusp. First lateral tooth with a small cusp on medial side only of a broad cusp. Distal lateral teeth of a single hooklike cusp, some with a small notch.

DISCUSSION. *Phyllaplysia zostericola* is larger than any of the other representatives of the genus. This form is extremely common in areas where it is found and therefore different from all other species which Marcus and Marcus (1957) state to be rare. *Phyllaplysia engeli* Marcus, 1955, claimed to be more plentiful than the others is not nearly as common as *P. zostericola* which may be collected by the thousands in less than an hour. As in *P. engeli* the genital opening lies outside the branchial cavity, not within it as in *P. lafonti* (P. Fischer, 1870). *Phyllaplysia paulini* Mazarelli, 1895, is green with white stripes, but *P. zostericola* has obvious black stippling which makes the lines appear black instead of white. It does not have the secondary shell that is found in *P. engeli*.

The genus *Phyllaplysia* was established by P. Fischer in 1872 with *P. lafonti* (Fischer, 1870) as the type species. Marcus (1955) lists the following representatives of the genus: *P. paulini* Mazarelli, 1895; *P. brongniartii* (Blainville, 1825) Engel, 1934; *P. ornata* (Deshayes, 1853) Fischer, 1872; *P. depressa* (Cantraine, 1835) *sp. inq.; P. viridis* (Bergh, 1905); *P. varicolor* (Bergh, 1905); *P. plana* Eales, 1944; and *P. engeli* Marcus, 1955. None of the above is from North American waters.

Phyllaplysia zostericola is found living on the leaves of *Zostera marina* in the protected waters of many of the bays along the west coast of North America. In addition to the type location of Mitchell Bay in San Juan County, Washington, several other locations in the San Juan Archipelago have the form in great quantities. I have collected it in Puget Sound, Washington, in the vicinity of Bremerton in Dye's Inlet, and near the northern

city limits of Seattle. I have also collected it in Newport Bay, near Balboa Island in southern California. The form is well known from Elkhorn Slough near Monterey, California (MacGinitie, 1939; Ricketts and Calvin, 1948), and from Tomales Bay north of San Francisco, California, where Smith *et al.* (1954) report it to be more common than at Elkhorn Slough. I have searched the bays of the Oregon Coast very carefully and have failed to find the form though the habitat appears to be similar to that found in both Puget Sound and California.

The detailed morphological description which follows is based on dissection and observation of many specimens. The morphological nomenclature is after Eales (1921).

DETAILED MORPHOLOGY

The adult of *P. zostericola* is about 5 cm. long and 1 cm. wide. Sexually mature individuals vary greatly in size, and individuals from one locality may differ in size from those from another locality.

The general outline of the body is elliptical. It is more flattened than most of the other members of the Apysiidae, but retains the hump in the region of the pallial eavity. The soft body is covered with a layer of mucus. Superficially the animal appears to be bilaterally symmetrical, but has the torsion of a gastropod. The surface of the animal is smooth, without papillae.

The color dorsally is the same green color as the eelgrass, being a little lighter along the margins of the foot. The dorsal surface of the body is marked with longitudinal white lines having black stippled margins. These lines vary from individual to individual and do not appear to have a definite pattern. There are also finely stippled transverse black lines over most of the rest of the dorsal surface. There is a thin white line, not bordered with black stippling about $\frac{1}{2}$ mm. from the lateral margin of the foot on the dorsal surface of the body. The pigmentation is somewhat darker at the anterior end. The longitudinal markings blend with the veins of the *Zostera* on which the animal lives, and give excellent protective coloration. The ventral surface of the foot, a pale green somewhat the color of the inside of a cucumber, has no markings. The internal organs are slightly visible through the translucent foot.

The anterior portion of the body bears two pairs of appendages which give the animal the appearance of having ears and a grotesque snout. The anterior tentacles (*tent.*) are a continuation of the tissues which extend anterolaterally from the head. They are leaflike in shape and contractile. In preserved specimens they are much contracted and difficult to see, but readily observed

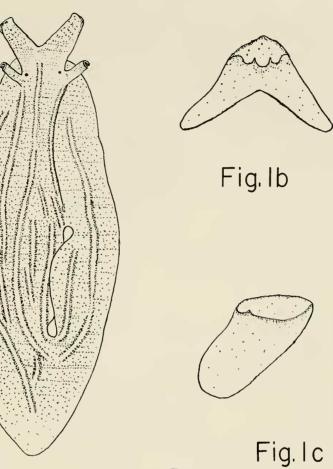
Figure 1a. Dorsal view of a living animal from a projected photograph.

Figure 1b. Rachidian tooth of radula.

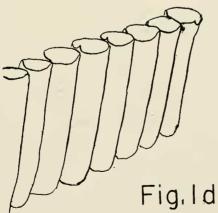
Figure 1c. First left lateral tooth of radula.

Figure 1d. Eight distal teeth on right side of radula.

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in living specimens. A lateral groove lined with cilia passes obliquely across the tentacles from the anteromedial to posterolateral. One immature specimen exhibited rhythmic contractions of these tentacles.

The posterior pair of appendages, the rhinophores (rh.), are also highly contractile and in preserved specimens difficult to observe. They move about freely and are probably chemoreceptors. Each rhinophore also has a ciliated groove which causes a current to flow from the distal to the proximal end of the structure. The outer tip of the rhinophore is horseshoe-shaped, the opening of the horseshoe being posterolateral and continuous with the groove.

The paired eyes (ey.) lie anterior to and at the base of the rhinophores. Each appears as a pigmented spot on a small papilla.

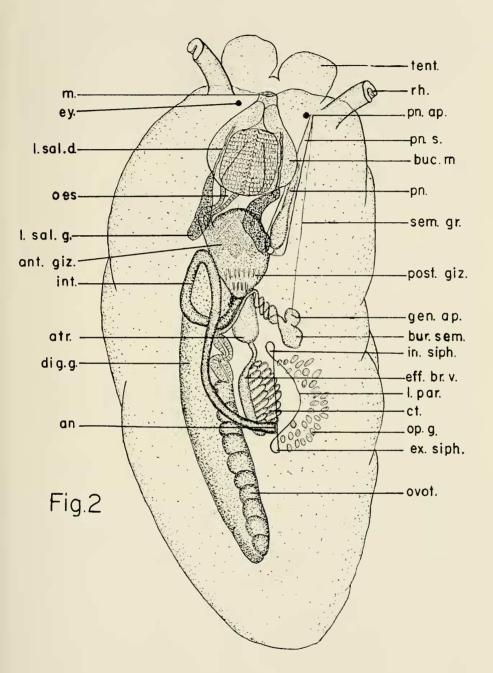
Ventral to the right rhinophore the opening of the penis cavity (pn. ap.) marks the anterior end of the seminal groove (sem. gr.). The walls of the groove are composed of lateral folds of the epidermis which form a more or less closed channel. It passes posteriorly from the opening of the penis sheath, lateral to the right rhinophore, and terminates at the common genital aperture (gen. ap.) on the dorsal surface of the right side of the body about half way back.

In the posterior half of the body on the right side the parapodia (*l. par.*) lateral reflections of the foot, are apparently fused to the dorsolateral body walls and meet over the pallial cavity. The right parapodium lies dorsal to the left. The pallial cavity lies just posterior to the common genital aperture, bounded on the right by the right parapodium, on the left by the mantle, ventrally by the inner wall of the foot, dorsally by the overlapping parapodia, and anteriorly and posteriorly by the junctions of the right parapodium and the mantle.

Openings of the pallial cavity at the anterior and posterior ends are formed by gaps left by the overfolding of the parapodia. These gaps form an anterior incurrent siphon (in. siph.) and a posterior excurrent siphon or opening (ex. siph.). When narcotized with urethane or placed in water low in oxygen, the siphons are enlarged by a separation of the flaps.

Several structures are contained within the pallial cavity, the most prominent of which is the ctenidium (ct.). It lies with its axis longitudinally directed, its posterior end being a bit more distant from the midline of the

Figure 2. Dorsal view of a stained and cleared juvenile about 15 mm. long. The abbreviations used in this figure indicate structures as follows: *an.*, anus; *ant. giz.*, anterior gizzard; *atr.*, atrium; *buc. m.*, buccal mass; *bur. sem.*, bursa seminalis; *ct.*, ctenidium; *dig. g.*, digestive gland; *eff. br. v.*, efferent branchial vein; *ex. siph.*, excurrent siphon; *ey.*, eye; *gen. ap.*, genital aperture; *in. siph.*, incurrent siphon; *int.*, intestine; *l. par.*, left parapodium; *l. sal. d.*, left salivary duct; *l. sal. g.*, left salivary gland; *m.*, mouth; *as.*, espohagus; *op. g.*, opaline gland; *ovot.*, ovotestis; *pn.*, penis; *pn. ap.*, penial aperture; *pn. s.*, penis sheath; *post. giz.*, posterior gizzard; *rh.*, rhinophore; *sem. gr.*, seminal groove; *tent.*, tentacle.



animal than the anterior end. It is composed of a single primary "trunk" which gives off parallel much-folded branches, which become progressively smaller in an anteroposterior direction. At the base of the ctenidium, on the right side, is the osphradium.

The pullial cavity also contains the terminal openings of the digestive and the excretory systems. The anus (*un.*) lies on the posterodorsal margin of the mantle, and during defectation the anus and a portion of the surrounding mantle are extended out through the excurrent siphon. The pore of the excretory system opens medial to the anterior attachment of the ctenidium and on the ventral side of the mantle fold.

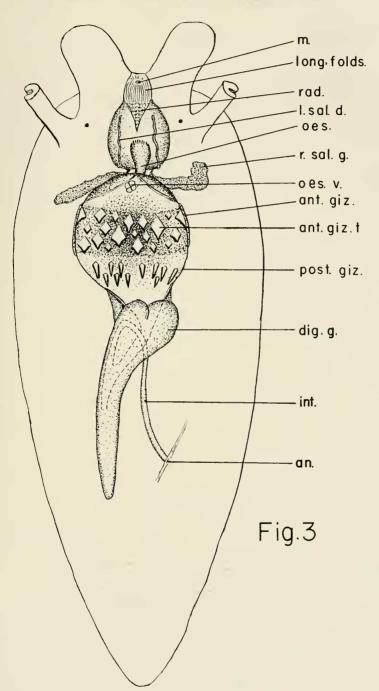
The pallial eavity receives the secretions from two sets of glands. The large unicellular opaline glands lie in the tissue ventrolateral to the pallial cavity. They stain deep purple with hematoxylin. Their function has not been determined in *P. zostericola*, but in *Aplysia punctata* (Eales, 1921) they are supposed to secrete a protective fluid. The other glands in the pallial cavity are the smaller unicellular "purple glands." These lie on the ventral side of the tip of the mantle and stain pink with triosin. Their function is not known in *P. zostericola*, but in *A. punctata* they also secrete a purple protective fluid when irritated. *Phyllaplysia zostericola* has been observed to secrete only a milky fluid into the water.

On the ventral surface of the body at the anterior end, the mouth (m.) is the only prominent structure. Located ventrally just posterior to the notch between the anterior tentacles, it consists of an oval opening surrounded by longitudinal folds. When feeding, the size of the opening is increased uniformly in all directions, and the radula is extended through this enlarged opening.

On the ventral surface of the animal posterior to the mouth there is a transverse fold called the gutter which is commonly taken to delimit the head. Posterior to the gutter is the foot.

The entire surface of the foot is covered with eiliated epithelial cells interspersed with many gland cells. The anterior end of the foot is truncated but not notched, and the posterior end, roughly triangular, extends beyond the visceral hump to form a "tail."

Figure 3. Diagram of the digestive system. The abbreviations used in this figure indicate structures as follows: an, anus; ant. giz, anterior gizzard; ant. giz. t, anterior gizzard teeth; dig. g, digestive gland; int, intestine; long. folds, longitudinal folds; l. sal. d, left salivary duct; m, mouth; σs , esophagus; σs . v, esophageal valve; post. giz, posterior gizzard; rad, radula; r. sal. g, right salivary gland.



DIGESTIVE SYSTEM (Figure 3.)

The digestive system of P. zostericola is similar in most respects to that of other gastropods. The mouth leads into the buccal cavity from which the esophagus (as.) arises. The esophagus continues posteriorly through the ganglionic ring, then opens into a thin-walled erop which in turn is continuous with the muscular heavy-walled gizzard (ant. giz.). The gizzard contains teeth (ant. giz. t.) which almost fill the lumen of the digestive tract at this point. The posterior part of the gizzard (post. giz.) is pouchlike and communicates posteriorly with the digestive gland (dig. g.) and intestine (int.). The intestine terminates posteriorly at the anus (an.). The glands of the digestive system include the digestive gland lying along the left side of the visceral mass, and the paired salivary glands (l. and r. sal. g.) lying on the dorsal surface of the stomach.

1. Mouth. The mouth (m.) lies on the ventral surface between the anterior tentacles. It is surrounded by about 15 longitudinal folds (long, folds) which, together with the oral sphincter, permit the opening to be enlarged. Posterior to the longitudinal folds the walls of the oral cavity are lined with a layer of elongate epithelial cells, each with a conspicuous basal nucleus. The apex of each cell is crowned with noncellular horny material which appears to be a secretion of the cells. Eales (1921) calls these "stick cells." The horny material, in some areas thicker than the cellular layer, fuses to form the mandibular plate. The anterior part of the oral cavity is lined with this mandibular plate, but the plate does not extend posteriorly beyond the point of origin of the œsophagus. The mandibular plate extends lateroventrally to the odontophore. At no place does the odontophore contain stick cells or their horny secretion.

The odontophore lies in the center of the oral cavity with its anterior edge well within the mouth. The muscles which operate it are inserted inferiorly and posteriorly on the cartilaginous part of the odontophore. This cartilagelike structure is subspherical in shape and is covered dorsally and laterally by the radular sac. A median furrow on the dorsal and anterior surface of the odontophore contains the radula (*rad.*). Lateral furrows on either side of the median furrow limit the width of the radula.

The radula has from 40–41 rows of teeth consisting of 42–52 lateral teeth on either side of a rachidian tooth. The rachidian tooth (fig. 1b) has a central cusp flanked on either side by one small lateral cusp. The base of the rachidian tooth has two legs. The lateral teeth next to the rachidian tooth (fig. 1c) bear a small cusp distal to a broad cusp, but the rest of the lateral teeth (fig. 1d) have a single cusp though an occasional cusp will appear notched.

2. Salivary Glands. Paired tubular salivary glands lie on the dorsolateral surface of the stomach. The right gland (r, sal, g.) is somewhat larger than the

left (l. sal. g.). Small tubular salivary ducts (l. sal. d.) extend anteriorly in contact with the α sophagus, passing lateral to the point of emergence of the α sophagus, and open into the top of the buccal cavity.

3. Oesophagus. After emerging from the dorsal surface of the buccal mass, the æsophagus ($\alpha s.$) turns abruptly downward, passes through the ganglionic ring, and then continues posteriorly. It enters the ventral portion of the erop through a four-flapped valve ($\alpha s. v.$). The walls of the æsophagus are heavy longitudinal folds lined with a thickly ciliated epithelium.

4. Stomach. The stomach is divided into three parts, the erop, anterior gizzard (ant. giz.), and posterior gizzard (post. giz.). The erop, a thin-walled sae posterodorsal to the ganglionic ring, is lined with nonciliated cells which differentiate it from the æsophagus. The wall consists of epithelium surrounded by a circular layer of muscles. The erop is continuous posteriorly with the anterior gizzard, a structure of approximately the same external diameter. The anterior gizzard, however, is surrounded by an exceptionally heavy circular layer of muscle and contains about 15 chitinous teeth (ant. giz. t.). These teeth, arranged in sockets, arise from cells similar to the stick cells of the mandible. In the preserved specimens the teeth can easily be removed from the sockets. The sockets appear to be undercut on the margins, and the epithelium between the sockets and covering the undercut surface is greatly folded.

The posterior gizzard is continuous with the anterior gizzard, but lacks the large teeth of the latter. There are, however, about twelve long narrow toothlike spines projecting from the walls. The lining of the posterior gizzard appears to be a continuation of the inter-socket lining of the anterior gizzard. The wall of the second gizzard is composed of a layer of cuboidal cells surrounded by a thin circular layer of muscle. The posterior gizzard is fused ventrally to a median strand of longitudinal muscles.

5. Digestive Gland. The digestive gland (dig. g.) lies on the left side of the body and extends posteriorly from the stomach along the left side of the visceral mass. Its cavity is continuous with the stomach cavity. It contains numerous channels that pass into the tissues, some end blindly, and others anastomose to form a network of canals. The intestine emerges from the anterior part of the digestive gland and is continuous with the main cavity of the gland. The cavities of the digestive gland are lined with cuboidal gland cells, each with a basal nucleus.

6. Intestine. Immediately after its origin from the digestive gland, the intestine (int.) extends anteriorly, then turns 180 degrees to the right and proceeds posteriorly to the anus (an.). It is lined with a folded layer of eiliated columnar epithelial cells which are enveloped within a thin circular layer of muscle. The anus is provided with a sphincter.

CIRCULATORY SYSTEM (Figure 4.)

1. *Heart*. The two-chambered heart, located dorsally on the right side of the body, is anterior to the pallial cavity. It lies obliquely across the surface of the visceral mass; the anterior part is near the midline, and the posterior part is somewhat to the right of the midline. It lies so near the surface of the body that the heartbeat can be observed with transmitted light.

The posterior chamber of the heart, the atrium (atr.), is a thin, reticulate, spherical sac open at both ends. It opens into the ventricle (*ventr.*) anteriorly and receives the efferent branchial vessel (*eff. br. v.*) posteriorly. Its walls are thin, composed of a single layer of flattened cells, interspersed with small muscle cells. A few muscle fibers extend across the cavity.

The anterior chamber of the heart, the ventricle (*vent.*), is a heavy retieulate saclike structure shaped like a truncated cone, with the smaller end anterior. It is connected posteriorly with the atrium and anteriorly with the saclike aorta. The walls of the ventricle, more muscular than the walls of the atrium, are composed of a single layer of flattened cells with scattered muscle strands among them. The cavity of the ventricle contains many muscle fibers which stretch across it from wall to wall.

The heart lies in the pericardial sinus, a cavity much larger than the heart itself. The sinus communicates posteriorly with the kidney through the renopericardial duct.

2. Arterial System. Anterior to the ventricle a thin-walled, saelike vessel, the common aorta (com. ao.) serves as a common artery for all the blood that leaves the heart and gives rise to four large arteries:

a. Abdominal aorta (adb. ao.). This artery leaves the common aorta posteriorly and passes along the dorsal surface of the digestive gland. More posteriorly and to the right, the abdominal aorta divides into three arteries. The most anterior of these is a small vessel which runs to the little hermaphroditic duct (*lit. herm. d. a.*). The middle branch goes to the hermaphroditic gland (*herm. a.*), bifurcating before it enters the tissues. The posterior branch goes to the hermaphroditic gland without dividing. Within the hermaphroditic gland the arteries divide repeatedly to supply all the lobes of the gland.

Figure 4. Diagram of the circulatory system. The abbreviations used in this figure indicate structures as follows: *abd. ao.*, abdominal aorta; *ant. ao.*, anterior aorta; *ant. gen. a.*, anterior genital artery; *ant. pn. a.*, anterior penial artery; *atr.*, atrium; *com. ao.*, common aorta; *eff. br. v.*, efferent branchial vein; *g. as. a.*, gastro-æsophageal artery; *herm. a.*, hermaphroditic artery; *l. herm. d. a.*, large hermaphroditic-duct artery; *ped. a.*, pedal artery; *peribuc. a.*, peribuccal artery; *post. pn. a.*, posterior penis artery; *rh. a.*, rhinophore artery; *spct. a.*, spermatocyst artery; *spth. a.*, spermathecal artery; *ventr.*, ventricle; *vulv. a.*, vulvar artery.

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b. Genital artery. The genital artery originates from the common aorta and extends laterally to the right. It soon bifurcates, giving rise to two large branches, one of which turns posteriorly, the other anteriorly.

The posterior branch runs along the oviduet supplying about eight small branches in succession to the oviduet and one small artery to the seminal receptacle (*spct. a.*). It also gives off branches in the tissues of the mucous gland and then passes to the foot where it could no longer be traced.

The anterior branch of the genital artery (*ant. gen. a.*) extends anterolaterally along the oviduct to the bursa seminalis where it gives rise to a small branch to the spermatheea. It then continues laterally along the large hermaphroditic duet and divides into one ventral and two dorsal arteries (*vulv.* a.) to the vagina.

e. Gastro-æsophageal artery $(g. \, \alpha s. \, a.)$. The gastro-æsophageal artery arise from the common aorta and passes anteriorly and to the left giving off a branch to the right surface of the stomach, a branch to the ventral surface of the digestive gland, and then continues on to the left surface of the stomach. The artery to the digestive gland enters the ventral surface and gives off a small artery to the left body wall. The right and left gastric arteries continue anteriorly along the lateral surfaces of the stomach, giving rise to two branches to the stomach wall and small branches to the salivary glands.

d. Anterior aorta (ant, ao.). The anterior aorta arises from the anterior and right side of the common aorta. The first branch to separate is a small dorsal vessel to the spermatheca (spth. a.). Next a branch enters the right body wall. The main portion of the anterior aorta continues medioventrally beneath the ganglionic ring, giving rise to two branches (ped. a.), one to either side of the body to the tissues of the foot. The anterior aorta then gives off two small arteries to the right which supply the penis sheath (ant. pn. a. and post. pn. a.) and one to the left which runs to the region behind the rhinophore. The anterior aorta then enters the buccal mass and gives a branch laterally to either side of the buccal mass (peribuc. a.) and a branch to each rhinophore (rh. a.).

3. Venous System. There are no capillaries in P. zostericola, so that the function of getting blood to the tissues is accomplished by many ill-defined sinuses which constitute the hemocoel. In the absence of true veins, several sinuses in the vicinity of the pallial eavity return blood to the etenidium, from which it returns to the heart. Blood flows from the ctenidium to the atrium by way of the efferent branchial vessel (*eff. br. v.*).

RESPIRATORY SYSTEM.

(Figure 4.)

The respiratory system consists of the single asymmetrically placed ctenidium (ct.) typical of the tectibranchs. It is a highly convoluted sac located in the pallial cavity, attached anteriorly and medially. Water passes over the ctenidium by ciliary action, enters the anterior incurrent siphon (in. siph.) and passes out the posterior excurrent siphon (cx. siph.). The ctenidium is continuous with the atrium of the heart anteriorly by means of the efferent branchial vessel (eff. br. v.), thus providing for aeration of the blood immediately before it passes into the heart. Medially the ctenidium is continuous with the sinuses associated with the kidney.

The walls of the etenidium, composed of a thin epithelium, are supported by scattered strands of muscle fiber. Isolated cells in the interior of the etenidium (in cross sections) may be either amoeboid cells or sections of minute muscle or nerve cells. When a drop of fixative or other toxic substance is added to the medium, the ctenidium is rapidly withdrawn into the mantle cavity, indicating muscle tissues in the ctenidium.

The surface of the ctenidium has small scattered ciliated brushes, which may be sensory and aid the osphradium. Near the base of the ctenidium, tissues of unknown function appear to be quite glandular.

EXCRETORY SYSTEM.

The excretory system consists of a single asymmetrically placed kidney embedded in the mantle tissues which overlie the visceral mass. It is a subtriangular sac lying to the right of the midline with the base along the margin of the mantle and the apex dorsal to the atrium. The inner walls are composed of a single layer of large cuboidal cells, folded into many parallel lamellae which project into the lumen. Anteriorly this sac opens into the pericardial canal which is lined with cells bearing long cilia. Posteriorly the kidney opens into the mantle cavity through the excretory pore at the posterior edge of the base of the ctenidium. The cavity of the kidney and the pericardium constitute a part of the true coelom.

NERVOUS SYSTEM. (Figure 5.)

The central nervous system consists of the paired cerebral, pedal, and pleural ganglia, constituting the circumœsophageal ganglionic ring; the unpaired visceral and parietal ganglia; and the paired buccal ganglia.

1. The Buccal Ganglia and Nerves. The buccal ganglia (buc. g.) on the posterior wall of the buccal mass ventral to the point of origin of the œsophagus, consist of two ovoid ganglia connected medially by a short commissure. They connect posteriorly to the cerebral ganglia by the cerebrobuccal connectives which pass laterally from the buccal ganglia and turn posteriorly and dorsally to enter the anterior surface of the cerebral ganglia. The buccal ganglia give rise to the following nerves:

a. The single radular nerve (B-1) arises from the midpoint of the buceal commissure and passes anteriorly along the dorsoposterior surface of the buceal mass. Rami run to either side of the buceal mass.

b. The paired ventral pharyngeal nerves (B-2) extend anteriorly from the lateral portion of the buccal ganglia and enter the ventral wall of the buceal mass.

c. The paired dorsal pharyngeal nerves (B-3), larger than the ventral pharyngeal nerves, pass anteriorly from the lateral tip of the buccal ganglia around the lateral walls of the buccal mass. Each divides into two rami which penetrate the tissues of the buccal mass.

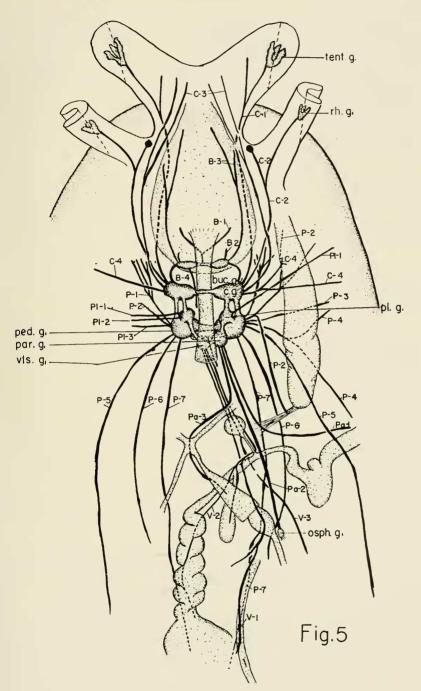
d. The salivary gland nerves (Eales, 1921) were not found, but examination of the serial sections revealed both salivary glands in contact with the buceal ganglia, and the possibility that small nerves run to the glands eannot be excluded.

e. The gastro- ∞ sophageal nerve (*B-4*) is a large unpaired nerve which arises from the left buceal ganglion, courses posteriorly with the ∞ sophagus, and then penetrates the anterior gizzard.

2. The Cerebral Ganglia and Nerves. The paired cerebral ganglia (c. g.) lie dorsal and lateral to the œsophagus and are joined by the cerebral commissure which crosses the œsophagus dorsally. They are connected to the buceal ganglia by the cerebro-buceal connectives, to the pedal ganglia by the cerebro-pedal connectives, and to the pleural ganglia by the cerebro-pleural connectives. The cerebro-pedal and cerebro-pleural connectives extend posteroventrally, lateral to the œsophagus. The cerebro-pleural is medial to and slightly above the cerebro-pedal. Nerves which arise from the cerebral ganglia are as follows:

a. The paired tentacular nerves (C-1) are the most anterior nerves to arise from the cerebral ganglia. Each extends anteriorly from its ganglion, beneath the outer edge of the buccal mass to the anterior tentacles. It bifureates at the level of the posterior margin of the tentacles and both rami penetrate the tentacles. The median ramus innervates the muscular tissue of the tentacles. The lateral ramus passes to the inner edge of the lateral sulcus and forms a four-lobed ganglion (*tent. g.*). Two lobes extend, one on either side

Figure 5. Diagram of the nervous system. The abbreviations used in this figure indicate structures as follows: *buc. g.*, *buccal* ganglion; *c. g.*, cerebral ganglion; *osph. g.*, osphradial ganglion; *par. g.*, parietal ganglion; *ped. g.*, pedal ganglion; *pl. g.*, pleural ganglion; *rh. g.*, rhinophore ganglion; *tent. g.*, tentacular ganglion; *vis. g.*, visceral ganglion. Nerves are labeled numerically from each ganglion as *C-1*, *C-2*, etc.; those from the cerebral ganglion as *C-1*, *C-2*, etc.; those from the pleural ganglion as *Pl-1*, *Pl-2*, etc.; those from the pedal ganglion as *P-1*, *P-2*, etc.; and those from the visceral ganglion as *V-1*, *V-2*, etc.



of the sulcus, a third lobe lies along the inner edge of the sulcus, and the fourth lobe lies proximally along the nerve.

b. The paired rhinophore nerves (C-2) arise from the cerebral ganglia and are combined rhinophore and optic nerves. These nerves leave the ganglia laterally as single strands and pass anteriorly along the inner dorsolateral body wall. Each nerve bifurcates, giving rami to the eyes and the rhinophores. On the left this bifurcation is near the point of entrance of the nerve into the rhinophore, but on the right the bifurcation is far proximal, near the point of origin of the nerve from the cerebral ganglion. In this case, however, the two nerves course through the same connective tissue to the base of the rhinophore. The larger of the two rami goes to the rhinophore where it gives rise to the three-lobed rhinophore ganglion (rh. g.) similar to the ganglia described for the tentacles. The optic ramus passes to the posterior part of the eye and terminates in a layer of cells around the eye which appear to be the same tissue as the sensory ganglia in the rhinophore.

c. The paired labial nerves (C-3) arise from the lateral surfaces of the cerebral ganglia and extend anteriorly, lateral to the buccal mass. They bifurcate at the level of the base of the rhinophores and send rami to the area between the tentacles.

d. The paired cerebro-lateral nerves (C-4) arise from the lateroventral surfaces of the cerebral ganglia and pass laterally to the walls of the body at the vertical of the cerebral ganglia. The left nerve is uniramus; the right divides and sends a small branch to the penis sheath.

e. Minute paired static nerves run from the cerebral ganglia to the statocysts which are embedded in the anterior walls of the pedal ganglia.

3. The Pleural Ganglia and Nerves. The pleural ganglia (pl. g.) lie dorsal to the pedal ganglia, connected to them by the short pleuro-pedal connectives and to the cerebral ganglia by the cerebro-pleural connectives. There is no commissure between the pleural ganglia. The left pleural ganglion is connected posteriorly to the visceral ganglion by a pleuro-visceral connective, and the right pleural ganglion is connected posteriorly to the parietal ganglion by the pleuro-parietal connective. The pleural ganglia give rise to the following nerves:

a. The paired first pleuro-lateral nerves (Pl-1) arise from the lateral surfaces of the pleural ganglia and pass laterally to the body wall. The right nerve innervates the tissues anterior to the common genital aperture and the left terminates at a similar location on the left side of the body.

b. The unpaired second pleuro-lateral nerve (Pl-2) arises from the left pleural ganglion and courses with the first pleuro-lateral nerve. As far as can be detected, the two nerves terminate at the same point in the tissues. No counterpart was found on the right side.

4. The Pedal Ganglia and Nerves. The pedal ganglia (ped. g.) are the

largest of the ganglia in *P. zostericola* and lie lateral and ventral to the œsophagus. They are connected to the cerebral and pleural ganglia by the cerebropedal and pleuro-pedal connectives respectively as noted above. Two commissures run between the pedal ganglia; the pedal commissure, which is a broad band that passes ventral to the œsophagus, and the parapedal commissure, which is a small thread ventral to the aorta. The nerves arising from the pedal ganglia from anterior to posterior are:

a. The paired anterior pedal nerves (P-1) pass cephalad from the lateral wall of the pedal ganglia, each having four rami to the anterior portion of the foot.

b. The small, paired, first, pedal-lateral nerves (P-2) originate in the lateral walls of the pedal ganglia and pass anterolaterally to the body wall. The left one is small and can be followed only a short distance, but the right one is larger and can be traced to the right body wall. The right nerve gives off a branch to the penis retractor muscle, and continues laterally to supply two rami to the body wall lateral to the penis.

c. The paired, second, pedal-lateral nerves (P-3) are quite small and extend from the lateral surface of the pedal ganglia to the body wall. The left nerve courses with the two lateral nerves from the pleural ganglion, the right passes ventral to the penis sheath and terminates in the body wall.

d. The unpaired, third, pedal-lateral nerve (P-4) arises from the lateral surface of the right pedal ganglion, passes ventral to the penis retractor muscle, and divides into two rami. One innervates the body wall anterior to the common genital aperture, and the other passes ventral to the common genital duct to terminate in the body wall between the common genital aperture and the pallial eavity.

e. The large, paired, fourth, pedal-lateral nerves (P-5) pass laterally from the lateral wall of the pedal ganglia, then turn sharply posterior to the parapodia. On the right the nerve passes ventral to the common genital duct.

f. The large, paired, middle pedal nerves (P-6) pass caudad from the pedal ganglia, through the tissues of the foot about halfway between the midline and the margin, to supply the middle portion of the foot.

g. The large, paired, posterior pedal nerves (P-7) arise from the posterior surface of the pedal ganglia, pass through the tissues of the foot on either side of the midline medial to the middle pedal nerves, and give off several small rami to the posterior portion of the foot. These nerves are the largest and longest in the body.

h. The small, unpaired, parapedal nerve arises from the parapedal commissure. It extends posteriorly, running beneath the anterior aorta in the connective tissue. It does not appear to be associated with the anterior aorta but with the connective tissue beneath it. This nerve arises from a point to the left of center of the parapedal commissure and appears to end in the connective tissue beneath the anterior aorta.

5. The Visceral Ganglion and Nerves. The visceral ganglion (vis. g.) lies ventral to the œsophagus, dorsal and medial to the left pedal ganglion, and posterior to the ganglionic ring. It is connected to the left pleural ganglion by the pleuro-visceral connective, and to the parietal ganglion by the visceroparietal connective. The latter is a short, wide band extending from the right side of the pleural ganglion to the left side of the parietal ganglion. The visceral ganglion gives rise to the following nerves:

a. The small abdominal nerve (V-1) arises from the posterior surface of the visceral ganglion, runs posteriorly to the right dorsal to the common genital ducts, then ventral to the kidney and pentrates the mantle to end in the region of the anus. A small ramus given off at the anterior border of the kidney courses through the connective tissue surrounding the medio-ventral edge of the renal organ.

b. The genital nerve (V-2) arises from the posterior surface of the viseeral ganglion, courses with the abdominal nerve to the region of the bursa seminalis, and gives off a branch to the spermatheca. The main trunk of the nerve follows the oviduet posteriorly, gives rise to a small ramus to the seminal receptacle, then continues posteriorly along the little hermaphroditic duet to the ovotestis.

c. The visceral nerve (V-3) arises from the posterior surface of the visceral ganglion and courses with the abdominal and genital nerves to the region of the large hermaphroditic duct. At the level of the common genital duct it diverges from the other nerves and continues into the floor of the pallial cavity where it ends.

6. *The Parietal Ganglion and Nerves.* The parietal ganglion (*par. g.*) lies posterior and dorsal to the right pedal ganglion and to the right of the visceral ganglion. It is connected to the visceral and right pleural ganglia by connectives. This ganglion gives rise to the following unpaired nerves :

a. The small vulvar nerve (Pa-1) arises from the posterior surface of the parietal ganglion, runs posteriorly around the base of the penis retractor muscle, then laterally to the right to terminate in the region of the common genital aperture.

b. The osphradial nerve (Pa-2) arises from the parietal ganglion, extends posteriorly to the anterior margin of the mantle cavity, where it enlarges to form the osphradial ganglion (osph. g.). From the osphradial ganglion several small rami extend posteriorly. One enters the ctenidium, while the others ramify into the tissues surrounding the ganglion.

c. The pericardial nerve (Pa-3) arises from the posterior part of the parietal ganglion medial to the osphradial nerve. It courses to the pericardium beneath the dorsal aorta.

The following nerves, present in related tectibranchs, were not located in *P. zostericola*:

a. Small parapodial nerves arising from the pedal ganglia and running

to the parapodia of *Aplysia punctata* (Eales, 1921) and to the body wall and parapodia in *A. cervina* and *A. dactylomela* (Hoffman, 1936). Mareus and Mareus (1957) report this to be the second nerve from the pedal ganglia in *Phyllaplysia engeli*.

b. A small pericardial nerve reported from the pedal ganglia to the aorta and dorsolateral body wall in *A. dactylomela* and *A. cervina* (Hoffman, 1936).

c. A small head retractor nerve going from the pedal ganglia to the head retractor muscle of *A. dactylomela* and *A. cervina* (Hoffman, 1936).

d. A small œsophageal nerve arising from the visceral ganglion and innervating the œsophageal artery in A. punctata (Eales, 1921).

e. A small spermathecal nerve from the parietal ganglion to the spermatheca in A. punctata (Eales, 1921).

Examination of histological sections reveal that all the ganglia of P. zostericola have peripheral nuclei. In the ganglia of the central nervous system the nonnucleated material is granular in appearance; in the peripheral ganglia it is much more homogeneous. The one exception to this is the osphradial ganglion in which the nonnucleated material is granular, resembling that in the central nervous system.

SENSE ORGANS.

1. Eyes (ey.). These appear as small black spots anterior to the base of the rhinophore. These spots are on slight elevations, but are not stalked. The structure of the eye is similar to that of *Hclix* (Cooke, Shipley, and Reed, 1927). It is essentially a spherical vesiele whose walls are formed by a single layer of sensory cells. A noncellular lens completely fills the chamber of the vesicle. The sensitive layer is composed of cells with basal nuclei which appear very much like the nuclei of the ganglia of the tentaeles and the rhinophores. The immediate apical portion of the cell is composed of clear evtoplasm that is similar in appearance to the perinuclear evtoplasm, but the portion of the cell between the apex and the nucleus is heavily pigmented. The pigmented area is continuous throughout all the cells of the sensitive layer except those cells that are in contact with the epithelium. These latter cells are unpigmented and compose the clear cornea. The pigmented layer is thickest opposite the corneal area and becomes gradually thinner nearer the cornea. The basal portion of the sensitive cells are in contact with a thin layer of nerve tissue that surrounds all the vesicle except the corneal layer. This nerve tissue is continuous with the threadlike optic nerve.

2. Osphradium. The osphradial ganglion of the branchial nerve lies lateral to the insertion of the etenidium. This ganglion, situated at the anterior incurrent portion of the pallial cavity, is covered with the epithelial lining of the pallial cavity. The osphradium is believed to be a water testing organ, and Eales (1921) reports that when contaminated water enters the pallial cavity

of *Aplysia*, the ctenidium is withdrawn and water is forcibly ejected from the pallial cavity. This ejection of water was not observed in *P. zostericola* though when a contaminant was added to the water the pallial cavity was closed for a short time.

3. *Statocysts.* These are small, thin-walled sacs on the anterodorsal surface of the pedal ganglion. These organs are connected to the cerebral ganglia by the microscopic static nerve. A statolith was not observed, but such a structure could easily have been lost in preparation.

REPRODUCTIVE SYSTEM.

(Figure 6.)

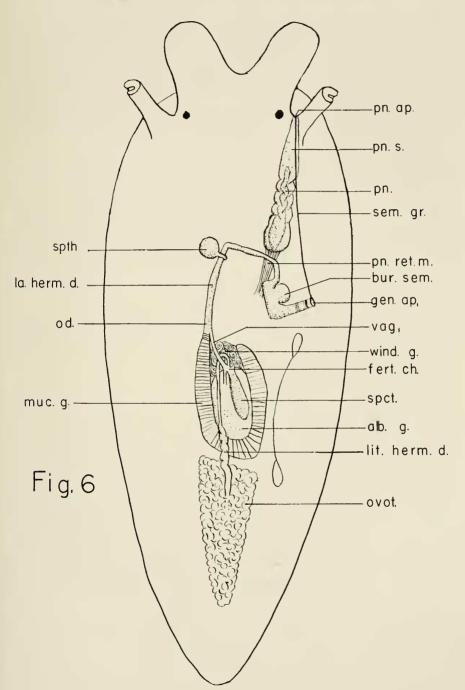
Phyllaplysia zostericola is a hermaphrodite. Not only are the two sexes represented by one individual, but the production of eggs and sperm is accomplished by the same organ. The reproductive system can be roughly divided into two parts: the male copulatory organ is located in a poeket which opens ventral to the right rhinophore, and the rest of the reproductive organs are located in the body cavity and communicate with the exterior through the genital aperture. The part of the reproductive system within the body cavity consists of the ovotestis; the accessory genital mass which includes the mucous gland, the albumen gland, and the spermatocyst or seminal receptacle: the bursa seminalis; and the ducts which connect these various organs.

The *ovotestis* (*ovot*.) produces both the eggs and the sperm, as the name implies. It is located in the posterior third of the visceral mass, is pale yellow, almost white in color, and looks very much like a thick eluster of very tiny grapes. It is included in a sheath which encases all the visceral mass, but can be easily separated from the rest of the mass when the sheath is removed.

The ovotestis is connected anteriorly by means of the *little hermaphroditic duct* (*lit. herm. d.*) to the accessory genital mass. The branches of this duct receive tubules from each acinus of the ovotestis. There are several coils midway in the little hermaphroditic duct. The anterior end of this duct is greatly reduced in diameter and runs without coiling to the fertilization chamber in the accessory genital mass. This chamber is located at the junction of the little hermaphroditic duct with the ducts from the accessory genital glands.

The accessory genital mass lies to the right of the anterior two-thirds of the visceral mass and ventral to the kidney. The mass contains the mucous

Figure 6. Diagram of the reproductive system. The abbreviations used in this figure indicate structures as follows: *alb. g.*, albumen gland; *bur. sem.*, bursa seminalis; *fert. ch.*, fertilization chamber; *gen. ap.*, genital aperture; *la. herm. d.*, large hermaphroditic duct; *lit. herm. d.*, little hermaphroditic duct; *muc. g.*, mucous gland; *od.*, oviduct; *ovot.*, ovotestis; *pn. penis*; *pn. ap.*, penial aperture; *pn. s.*, penis sheath; *pn. ret. m.*, penis retractor muscle; *sem. gr.*, seminal groove; *spct.*, spermatocyst; *spth.*, spermatheca; *vag.*, vagina; *wind. g.*, winding gland.



gland, the albumen gland, and the spermatocyst. The glands are rather tightly attached to each other and separation of them can be achieved only by careful dissection. The *spermatocyst* (*spet.*) lies on the surface of the albumen gland but not connected to it. It is a pale yellow, pear-shaped organ with the larger end posteriorly and the anterior end drawn into a thin duct which leads to the fertilization chamber. This organ serves as a seminal receptacle and in the inseminated individual is completely filled with motile sperm. Its walls are lined with a thin ciliated epithelium.

The albumen gland (alb. g.), a pale yellow gland lying in the middle of the visceral mass, is bounded laterally and posteriorly by the mucous gland. The albumen gland is a sac containing many irregularly arranged septa and can be differentiated from the surrounding mucous gland only by texture. It opens anteriorly through a small short duet into the fertilization chamber.

The mucous gland (muc. g.) is an irregular U-shaped organ lying around the lateral and posterior aspects of the albumen gland. This saclike gland contains many lamellate septa perpendicular to its walls. From its right arm, a highly convoluted tubule, the winding gland (wind g.), connects the mucous gland to the fertilization chamber. The walls of the convoluted portion of the mucous gland are greatly folded and lined with a thickly ciliated columnar epithelium. These coils lie on the anteroventral edge of the accessory genital mass to the right of the oviduet. The cellular lining of the entire mucous gland is composed of typical secretory cells with large basal nuclei. The left arm is attached directly to the oviduet.

The large hermaphroditic duct (la. herm. d.) leads anteriorly from the accessory genital mass to the common genital aperture (gen. ap.). It arises from the left arm of the mucous gland and the continuation of the fertilization chamber which extends anteriorly. In cross section it is actually only one channel, but folds of the lining provide dual channels. The part of the duct that arises from the mucous gland serves as the oviduct, while the part of the duct which communicates with the fertilization chamber is the vagina. A groove in the vaginal wall is continuous with the little hermaphroditic duct and is part of the route which the sperm takes from the ovotestis to the penis.

The large hermaphroditic duct passes anteriorly from the accessory genital mass as a straight tube for about one millimeter and then coils slightly. The spermatheeal duct arises in this coiled area. Slightly anterior to the common genital aperture the duct turns sharply to the right and takes an S-shaped route to the common genital aperture. Near the aperture the walls become more muscular. A *bursa seminalis* (*bur. sem.*) located in the lesser curvature of the bend near the aperture, is a spherical enlargement of glandular tissue. Near the common genital aperture two bands of muscle encircle the duct.

The *spermatheea* (*spth.*) is a spherical sac attached to the large hermaphroditic duct about halfway between the accessory genital mass and the com-

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mon genital aperture. It is attached to the duct by a thin tube which passes from the lateral side of the duct and curves around it dorsally to the spermatheca. The spermatheca lies attached to the pericardium anterior to the ventricle. The spermatheca is lined with a ciliated epithelium. It contains many quiescent spermatozoa and a considerable quantity of debris. As in *Aplysia* (Eales, 1921) the spermatheca probably functions as a receptacle for debris introduced with the sperm.

Leading anteriorly from the common genital aperture is the *seminal* groove (scm. gr.) previously described. This groove is ciliated and is continuous with the seminal groove that runs through the oviduct. At its anterior end the seminal groove enters the penial aperture and turns posterior to run along the dorsolateral side of the penis sheath. When it reaches the base of the penis it turns anteriorly and runs along the penis. The seminal groove is S-shaped when the penis is withdrawn, but straight when the penis is extended.

The penis (pn.) is enclosed in the penis sheath (pn. s.) whose external opening (pn. ap.) lies ventral to the right rhinophore. This sheath is a pocket in the skin and is attached posteriorly to the foot by the penis retractor muscle (pn. ret. m.). The penis itself is a cylindrical muscular organ that spirals about two and one-half turns, varying both in number of turns and direction of coiling, from animal to animal. The unarmed penis is attached to the base of the eversible sheath, and during copulation the base of the penis is actually a few millimeters outside of the body.

Copulation in *P. zostericola* is reciprocal. Two animals come together with the anterior parts of their bodies in juxtaposition so that each penial aperture is in contact with the common genital aperture of the other. Each inserts its penis into the common genital aperture of the other and the pair may remain in copulation for several hours.

Oviposition is accomplished by the eggs passing out of the common genital aperture and down the seminal groove in a mucous thread one or two eggs wide. The egg thread passes down to the post buceal gutter to a temporary notch formed in the anterior margin of the foot. By moving the anterior part of the body in an oscillating arc across the blade of *Zostera*, and moving backwards, the animal attaches the eggs in a flat packet. The notch in the anterior margin of the foot is evident only during oviposition. During the egg-laying process the tentacles are markedly contracted.

NATURAL HISTORY

Phyllaplysia zostericola is found in protected bays on the blades of the broad-blade eelgrass, *Zostera marina*. Here it spends most of its adult life browsing along the blades. The species moves very slowly and has not been observed to move backwards except during oviposition. When progressing along the blade of *Zostera* the entire muscular foot is in contact with the plant, and

the animal moves by first lengthening and narrowing the body with the posterior portion attached and then shortening and broadening the body with the anterior portion attached. When detached from the substratum the animal tends to curl so that the foot is concave. When trying to attach itself, the animal first makes contact with the anterior part of the foot and broadens that part until it becomes firmly attached. The rest of the foot is then placed in contact from anterior to posterior. Phyllaplysia zostericola has not been observed to swim as reported for Aplysia punctata and some related forms by Eales (1921). When moving from one blade of grass to another the animal releases its hold with the anterior part of the body but remains attached with the posterior tip. Thus attached, it elongates its body and explores the surrounding region for some suitable object on which to attach. It is not at all uncommon to see an animal four cm, in length attached by the posterior one-half cm. slowly moving its anterior end to and fro in search of a suitable place for attachment. In the aquarium the animal has been observed on numerous occasions to crawl inverted on the surface of the water, the foot in contact with the surface film, presumably a ciliary movement. This phenomenon has not been observed in the natural habitat.

From the available evidence, it appears that in Mitchell Bay, on San Juan Island, Washington, the life eycle is repeated once a year. In August mature individuals 40–50 mm. in length were found, but in late December only specimens less than 10 mm. in length could be found, and these were hidden between the bases of the blades of eelgrass. Although immature, these forms showed the shape and general appearance of the mature individuals. A trip to Mitchell Bay in the middle of March revealed individuals up to 20 mm. in length, still sexually immature. Before the last of June, sexually mature individuals were plentiful. Mature individuals were found laying eggs until late in September. The tentative conclusion that the form has an annual life cycle seems warranted. Development in Newport Bay, in southern California, seemed to be somewhat later than in Puget Sound, for specimens collected in May were no larger than the northern form in March.

The color of the animal is protective. The stippling blends so well with the venation of the *Zostera* that the animal is frequently overlooked in a cursory examination.

Phyllaplysia zostericola has not been observed to have any natural enemies in Puget Sound though MacGinitie and MacGinitie (1949) report that in Newport Bay it is eaten by the cone snail *Conus californicus*. Specimens kept in an aerated aquarium without filter were observed to harbor a small ciliate in the mucus.

An examination of the stomach contents and of the feees did not reveal much of the feeding habits for the food was too finely divided. Specimens maintained in the aquarium were observed to remove algal and baeterial growth accumulated on the side of the tank and would leave a trail of cleaned glass.

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